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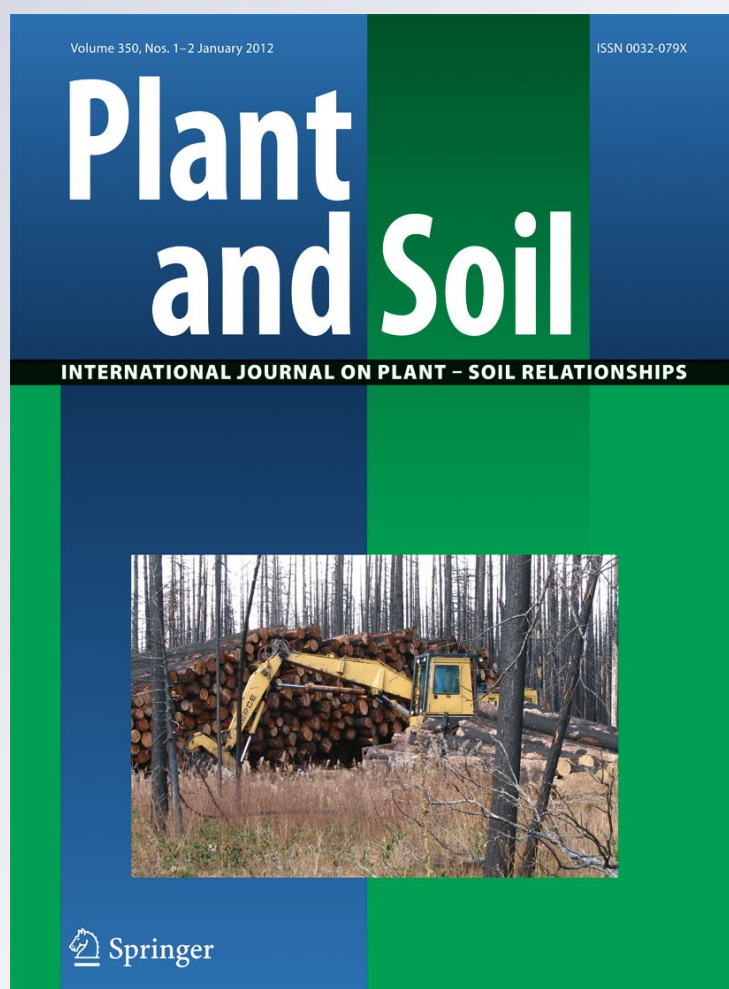
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Functional groups show distinct differences in nitrogen cycling during early stand development: implications for forest management

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Abstract

Background and aims Nutrient acquisition of forest stands is controlled by soil resource availability and belowground production, but tree species are rarely compared in this regard. Here, we examine ecological and management implications of nitrogen (N) dynamics during early forest stand development in productive commercial tree species with narrow (*Populus deltoides* Bartr. and *Platanus occidentalis* L.) and broad (*Liquidambar styraciflua* L. and *Pinus taeda* L.) site requirements while grown with a range of nutrient and water resources.

Methods We constructed N budgets by measuring N concentration ([N]) and N content (N_C) of above- and belowground perennial and ephemeral tissues, determined N uptake (N_{UP}), and calculated N use efficiency (NUE).

Results Forest stands regulated [N] within species-specific operating ranges without clear temporal or treatment patterns, thus demonstrating equilibrium between tissue [N] and biomass accumulation. Forest stand N_C and N_{UP} increased with stand development and paralleled treatment patterns of biomass accumulation, suggesting productivity is tightly linked to N_{UP} . Inclusion of above- and belowground ephemeral tissue turnover in N_{UP} calculations demonstrated that maximum N demand for narrow-sites adapted species exceeded $200 \text{ kg N ha}^{-1} \text{ year}^{-1}$ while demand for broad-site adapted species was below this level. NUE was species dependent but not consistently influenced by N availability, suggesting relationships between NUE and resource availability were species dependent.

Conclusions Based on early stand development, species with broad site adaptability are favored for woody cropping systems because they maintain high above- and belowground productivity with minimal fertilization requirements due to higher NUE than narrow site adapted species.

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Keywords Forest productivity · Net primary production · Nitrogen budget · Nitrogen uptake · Nitrogen use efficiency · Retranslocation · Short rotation woody crops

Abbreviations

N	nitrogen
N_{UP}	nitrogen uptake
NUE	nitrogen use efficiency
A_N	nitrogen productivity
[N]	nitrogen concentration
N_C	nitrogen content
NPP	annual net primary productivity
ST66	<i>Populus deltoides</i> clone of Mississippi origin
S7C15	<i>Populus deltoides</i> clone of east Texas origin
C	control treatment
I	irrigation treatment
F	fertilization treatment
IF	irrigation plus fertilization treatment
N_{MIN}	soil nitrogen mineralization
MRT	mean residence time
R_E	retranslocation efficiency
FUE	fertilizer use efficiency
N_{AV}	available nitrogen

Introduction

Forest production can be limited by nutrient and water availability. Nitrogen (N) is the most limiting mineral nutrient and forest growth is highly dependent on its availability (Binkley and Reid 1984; Fisher and Garbett 1980; Sayer et al. 2004). High N availability increases N uptake (N_{UP}), leaf N concentrations, leaf area, and litter production, which results in higher productivity (Coleman et al. 2006; Shan et al. 2001; Will et al. 2006). High N availability also improves leaf litter quality (Piatek and Allen 2001; Shan et al. 2001), and thus, N cycling. Nutrient availability influences belowground processes such as fine root production, turnover, soil CO₂ efflux, extracellular enzyme activity, and root exudation; however, the direction of N influence on these processes remains uncertain (Bradford et al. 2008; King et al. 2002; Phillips et al. 2008). Water is essential for fundamental plant processes and can influence nutrient uptake and availability in trees (Coyle and Coleman 2005; Linder 1989; Samuelson 1998) as adequate soil moisture is required for nutrient uptake and microbial processes (Kozlowski et al. 1991). Although species varying in nutrient requirements are expected to respond differently to combined nutrient and moisture availability,

multi-species studies using both fertilization and irrigation are rare (see Linder 1989).

Understanding N cycling and demand is critical to maximizing forest production (Fisher and Binkley 2000). Over the next 40 years, the land area dedicated to bioenergy crops and subsequent fertilizer use is projected to increase nearly 33-fold and 75-fold, respectively (Bouwman et al. 2010). The selection of material for production forestry favors rapidly growing species (or genotypes within a species) with robust site requirements where net primary productivity (NPP) and nitrogen use efficiency (NUE; the amount of biomass gained per unit N acquired) increase in parallel (Ragauskas et al. 2006). Selecting material with high NUE rates will reduce fertilizer requirements, and have many environmental benefits, including reduced potential for nutrient leaching (Binkley et al. 1999), reduced CO₂ emissions (Kara and Ozdilek 2010), and reduced negative impacts on soil microbiota (Rifai et al. 2010).

Assessing relationships between N dynamics and productivity requires accounting of both above- and belowground pools and fluxes (Berendse and Aerts 1987; Titlyanova 2007; Yuan et al. 2006). Assessment of standing root crop in relation to N_{UP} is rare, especially in forest systems (Nelson et al. 1995; Smethurst 2010). Most studies focus only on aboveground components despite the importance of including belowground pools and fluxes for understanding nutrient requirements (Norby and Jackson 2000). Although fine root pools are a small portion of total biomass, more than 80% of fine root standing crop turns over annually (Vogt 1991) and fine root lifespan can be less than one year in many tree species (Eissenstat and Yanai 1997). Thus, quantifying both standing root crop and turnover is critical to determine whole-plant nutrient budgets (Nelson et al. 1995). Side-by-side comparisons of complete forest stand N dynamics of multiple species receiving high and low resource amendments are, to our knowledge, unavailable and represent a major knowledge gap in production forestry (Smethurst 2010).

Tree species can be placed into functional groups based on site requirements (e.g., nutrient and water demand). Life history patterns pertinent to trees suggest necessary trade-offs between attributes allowing for successful competition (i.e., rapid exploitation of resources) and those allowing for successful stress tolerance (i.e., reduced but efficient exploitation)

(Grime 1977, 1979). Even among species grown for production purposes (i.e., good competitors), variation exists between stress tolerance and competitive ability. Examples of good competitors are narrow site adapted species such as eastern cottonwood (*Populus deltoides* Bartr.) and American sycamore (*Platanus occidentalis* L.) which rapidly colonize disturbed sites and require high resource availability. Cottonwood grows best on competition-free, moist, well-aerated, fine sandy or silt loams with sufficient nutrients (Cooper 1990; Dickmann and Stuart 1983; Stanturf et al. 2001). Sycamore, while intolerant of flooding during the growing season, grows best on sandy loam or loamy alluvial soils adjacent to rivers or stream banks with ample water supply (Wells and Schmidting 1990). Examples of stress tolerators are broad site adapted species such as sweetgum (*Liquidambar styraciflua* L.) and loblolly pine (*Pinus taeda* L.). Sweetgum is considered one of the most adaptable hardwood species as it tolerates a range of site conditions (Kormanik 1990; Nelson et al. 1995). Loblolly pine grows on a variety of soils, ranging from flat, poorly drained Coastal Plain to relatively dry Piedmont and upland areas (Baker and Langdon 1990). Based on broad site adaptation, forestry practitioners in the southeastern US prefer loblolly pine and sweetgum over cottonwood and sycamore due to the larger amount of land that can be utilized for plantations (Kline and Coleman 2010). Of particular interest here is understanding how species with narrow site requirements relate to those with broad site requirements in terms of indices of NUE.

The objective of this study was to examine ecological and management implications of N dynamics during early forest stand development in productive commercial tree species with narrow and broad site requirements while grown with a range of nutrient and water resources. Our study included treatments that regularly supplied nutrient and water amendments throughout stand development, and therefore altered long-term resource availability. We quantified annual N budgets, including assessment of tissue N concentration ($[N]$), N content (N_C), N_{UP} , and annual N losses through leaf litter and fine root turnover, to test the following hypotheses: 1) N_C increases in accordance with biomass accumulation, while $[N]$ remains static within a bounded operating zone; 2) species normally restricted to high resource environments have lower NUE than species with broad site requirements; 3)

regardless of functional grouping, all species respond to increased N availability with reduced NUE.

Materials and methods

This research is part of a long-term forest productivity project. Biomass accretion and allocation, NPP, radiation use efficiency, soil carbon dynamics, ice damage, sap flow, sap pH, and root respiration at this site have been previously reported (Allen et al. 2005; Aubrey and Teskey 2009; Aubrey et al. 2011, 2007; Coleman 2007; Coleman et al. 2004; Coyle and Coleman 2005; Coyle et al. 2008; Samuelson et al. 2009, 2008, 2007; Sanchez et al. 2007). The site, plant materials, and experimental design have previously been described in greater detail (Coleman et al. 2004; Coyle and Coleman 2005; Coyle et al. 2008). Growth, biomass, and NPP at this site were affected by species and resource amendments throughout early stand development (Coyle and Coleman 2005; Coyle et al. 2008). Both fertilization and irrigation elicited positive growth responses in cottonwood and sycamore, but the response to fertilization largely exceeded that of irrigation (Supplemental Table 1). Additive responses to the combination of fertilization and irrigation were commonly observed in all species. We observed fertilization, but not irrigation, responses in sweetgum and loblolly pine. Loblolly pine accumulated the largest amount of total biomass at age 4, followed by sycamore, sweetgum, and cottonwood. Annual NPP generally followed patterns similar to those of biomass accumulation in response to resource availability and among species. This study builds on previous NPP and biomass reports (Supplemental Table 2) and describes the dynamic changes in N pools and fluxes between trees and soil.

Site description and preparation

This short rotation woody crop experiment was conducted at the U.S. Department of Energy Savannah River Site, a National Environmental Research Park, located near Aiken, SC in the Carolina Sand Hill physiographic region (33° 23' N, 81° 40' E). The soil is predominately Blanton sand with loamy subsoil at 120 to 200 cm depth (Rogers 1990). We chose a site with uniform, deep sandy soil that provided low endemic soil moisture and N levels and employed

rigorous pest and competition control throughout the study. No other nutrient limitations besides N were apparent in soil or foliage tests. Thus, responses were not confounded with other factors, but were assumed to result from N and water amendments. In the spring of 1999, soil and debris from previous vegetation (i.e., plantation pine with oak understory), including stumps, were homogenized to a depth of 30 cm and lime was applied across the entire site for experimental consistency at a rate of 3.4 Mg ha⁻¹ to increase soil pH to 6.5 which was necessary for hardwood establishment. Initial soil physical characteristics and nutrient content can be found in the establishment report (Coleman et al. 2004; Tables 2–4 therein).

Plant material

American sycamore (Westvaco orchard run), sweetgum (Westvaco family WV340), and loblolly pine (International Paper family 7–56) bare-root seedlings were hand planted in February 2000. Hardwood cuttings of eastern cottonwood clones ST66 (Issaquena County, MS) and S7C15 (Brazos County, TX) were planted in April 2000. The inclusion of two cottonwood clones provided finer-scale differences within the species.

Experimental design

Each 0.22 ha plot contained a central 0.04 ha measurement plot with 54 trees planted at 2.5×3 m spacing. Trees outside the measurement plot were used for destructive sampling. The experiment was a split-plot arranged in a completely randomized block with each of three blocks containing a replicate of each species×treatment combination (see Coleman et al. 2004, Figure 5). Treatments were applied from April 1 to October 31 throughout the experiment and consisted of control (C), fertilization (F), irrigation (I), and irrigation+fertilization (IF). Drip irrigation (≤ 5 mm d⁻¹) was adjusted to meet evaporative demand and account for precipitation.

Cottonwood and sycamore received 40 kg N ha⁻¹ year⁻¹ in year 1, 80 kg N ha⁻¹ year⁻¹ in year 2, and 120 kg N ha⁻¹ year⁻¹ thereafter; sweetgum and loblolly pine received 40 kg N ha⁻¹ year⁻¹ in years 1 and 2, and 80 kg N ha⁻¹ year⁻¹ in years 3 and 4. Fertilizer increased to correspond with demand of growing trees—an approach that benefits growth and

reduces N leaching (Axelsson and Axelsson 1986; van Miegroet et al. 1994). Although different rates of fertilizer could potentially influence interactions between experimental factors (e.g., species, year, and fertilization), application rates were secondary to the plus or minus resource amendment question. Annual fertilizer treatments consisted of balanced macro- and micronutrients and were split among 26 weekly applications via drip irrigation that supplied additional water to flush drip tube lines (5 mm wk⁻¹). To maintain experimental consistency, C and F treatments also received 5 mm water wk⁻¹. Thus, non-irrigated treatments (i.e., C and F) received 130 mm of additional water annually compared to an annual mean of 494 mm for irrigated treatments (i.e., I and IF). Mean annual rainfall was 982 mm during the reporting period.

Growth, biomass, and NPP measurements

Growth and biomass were reported previously (Coyle and Coleman 2005; Coyle et al. 2008); a brief recount of methodology is presented here, as it is necessary for calculating N_C . Tree diameter was recorded annually. Whole-tree destructive harvests were conducted during dormancy after the 2000–2002 growing seasons for cottonwoods and sycamore, and after the 2001 and 2003 seasons for sweetgum and loblolly pine. Five trees were selected from each species×treatment combination at each harvest. Trees were stratified within each treatment based on diameter to include the entire size range for each species×treatment combination.

Aboveground biomass was separated into wood, bark, and branch (and leaf for loblolly pine) components. The entire tissue was collected in 2000 and 2001 and dry weights determined directly. In 2002 and 2003, we measured stem and branch (and leaf for loblolly pine in 2003) fresh weights and removed subsamples to determine water weight proportion. We determined dry weight as the product of fresh weight and water weight proportion. Bark was separated from wood in 5 cm segments at the top, middle, and bottom of each stem to determine the proportion of bark and wood.

Belowground biomass was separated into stump and coarse and fine root components. Stumps were removed using a mechanical tree spade (model TS34C, Bobcat Co., West Fargo, ND) that excavated

a 1 m diameter×0.69 m deep cone around the stump. Coarse roots (> 5 mm dia.) were separated from the stump. The stump was dried to a constant temperature and weighed in 2000 and 2001, but in 2002 and 2003, we measured fresh stump weight and determined water weight proportion from subsamples. Coarse root growth outside the tree spade cone was estimated by excavating three random 0.19 m² areas to 45 cm depth (see Coleman 2007 for details). This 45 cm depth was chosen because no roots with diameter > 5 mm were observed below 45 cm. Coarse roots were included without regard to tree of origin. This approach is comparable to whole-tree excavation (Resh et al. 2003).

We sampled fine root (< 5 mm) biomass at five random locations per plot each November from 2000 to 2003 (Coleman 2007). A 4.9 cm diameter push-tube removed soil cores from 0 to 15 and 15–45 cm depths. Mineral soil was washed from roots by elutriation (Gillison's Variety Fabrication, Inc., Benzonia, MI). Live roots were manually separated from dead organic matter, oven dried at 60°C, and weighed. We estimated 2002 sweetgum fine root biomass by interpolating between data from 2001 and 2003 collections.

Leaf litter was collected beneath five trees in each hardwood plot in fall 2000. In 2001, three baskets (56 cm wide×41 cm long×27 cm deep) were installed in each hardwood plot and litter was removed monthly from June to December. Loblolly pine litter was collected during winter. In 2001 and 2002, senesced foliage was retained on the stem, so litterfall was estimated from dead fascicles collected from each of 28 trees per plot. In 2003 and 2004, all litter from beneath five trees was collected. Samples were pooled within a plot, oven dried (60°C), and weighed.

We used fine root turnover data collected from cottonwood ST66 and loblolly pine from 2000 through 2003 (Coleman 2004; Coleman and Aubrey 2008). Minirhizotron observed roots were monitored until disappearance through the four-year period. Fine root turnover was predicted from survival functions calculated using the product limit estimate method in PROC LIFETEST (SAS, Version 9.1.3, SAS Inc., Cary, NC, USA). We assumed turnover was the inverse of median root lifespan (Majdi and Andersson 2005). Separate estimates were used for each treatment×year combination. Cottonwood S7C15, sycamore, and sweetgum were assumed to have the same

turnover rates as cottonwood ST66; the average for all treatment×year combinations was 0.87 gg⁻¹ year⁻¹. For loblolly pine, the average turnover rate for all treatment×year combinations was 1.10 gg⁻¹ year⁻¹. Fine root turnover likely differs among hardwood species, but turnover estimates derived on site from a hardwood yield better approximations than would estimates derived from pine or from other studies had they been available. Including even approximate measures of fine root turnover is critical for understanding forest carbon and N cycling.

Total biomass was determined by summing above- and belowground biomass components described above. Annual NPP was determined as the difference between total dormant season biomass of any given year and that of the previous year plus the annual amount of leaf litter and fine root turnover. In 2000, NPP was calculated as total biomass plus the annual amount of leaf litter and fine root turnover.

Nitrogen concentration and content measurements and calculations

Dried component tissue samples were ground through a 60-mesh screen. The small amount of fine root material collected with the push-tube precluded N analysis; therefore, we used fine roots sub-sampled from the coarse root collection. To determine foliar N status, hardwood foliage was collected annually each July. In 2000–2002, one sunlit, recently mature leaf was collected from each of the 54 measurement trees. In 2003, 6–18 fully expanded upper canopy leaves were collected from three trees within each plot. Loblolly pine foliage was sampled similarly in January following each growing season. Foliage samples were combined within each plot and oven dried (60°C). Both foliage and composite leaf litter samples were ground to pass through a 40-mesh screen and analyzed for [N] by dry combustion (Carlo-Ebra model NA-1500, Clemson Agricultural Service Laboratory).

We determined plot-level N_C based on each component tissue as the product of biomass and [N]. To estimate N_C for each perennial tissue fraction, we developed power functions to predict N_C as a function of diameter for each species×treatment combination (Coyle and Coleman 2005; Coyle et al. 2008; Parresol 1999). We used these regression parameters to calculate individual tree N_C from diameter and scaled

to the plot-level by summing component or composite values for all measurement-plot trees and dividing by measurement-plot area. Component values are individual tissues, whereas composite values are the sum of components for shoot (branch, bark, and wood, and leaf for pine), root (stump, coarse root, and fine root), and total (shoot and root). Leaf litter N_C was calculated as the product of leaf litter biomass and [N]. For hardwoods, growing season foliar N_C was calculated as the product of leaf litter biomass and foliar [N]. This approach potentially underestimated foliar N_C because dried litter likely weighs less than dried foliage; however, litter was collected monthly so changes in mass due to decomposition should have been minimal. For pine, foliar N_C was calculated as the product of foliage biomass and foliar [N].

To calculate N pools, fluxes, and indices, we used an approach described previously (Berendse and Aerts 1987; Calfapietra et al. 2007; Yuan et al. 2008). We calculated annual N_{UP} as the change in total N_C of dormant season biomass from 1 year to the next plus N_C of annual leaf litter and fine root turnover. NUE was calculated by dividing NPP by total N_{UP} . We also calculated the two components of NUE: N productivity (A_N) was calculated by dividing NPP by peak total N_C , and mean residence time (MRT) was calculated by dividing peak total N_C by annual N_{UP} . Retranslocation of N from senescing fine roots is generally considered negligible (Gordon and Jackson 2000; Nambiar 1987; but see Kunkle et al. 2009), so we focused only on foliar retranslocation. We calculated foliar N retranslocation as the difference between foliar N_C and litter N_C , and retranslocation efficiency (R_E) as foliar N retranslocation divided by foliar N_C .

Fertilizer use efficiency (FUE; the amount of N acquired per unit N available) was estimated as the quotient of annual N_{UP} and available N (N_{AV}). The amount of N_{AV} was estimated as the annual amounts of N applied via fertilization and soil N_{MIN} . We used N_{UP} in non-fertilized plots as a proxy for N_{MIN} rates. Within each block, C plot N_{UP} was assumed to approximate N_{MIN} for the C and F plot, and I plot N_{UP} was assumed to approximate N_{MIN} for the I and IF plot.

Statistical analysis

We analyzed age, species, and treatment effects using a multi-factorial repeated measures split-plot arranged

in a randomized complete block. Species was treated as the fixed whole-plot factor, year was treated as the fixed repeated factor, block was treated as a random factor, irrigation and fertilization were treated as fixed sub-plot factors, and plots were treated as experimental units. To model the correlation within experimental units over time, we analyzed each response using appropriate covariance structures (i.e., first-order autoregressive, Toeplitz, unstructured, compound symmetry, and variance component) and used AIC_C (Burnham and Anderson 1998) to determine which structure best fit each model. Denominator degrees of freedom were estimated according to the Kenward-Roger method (Kenward and Roger 1997). Treatment means were compared using Fisher's Least Significant Difference test. R_E was a proportional value and presented as such; however, the analyzed data were arcsine square root transformed (Zar 1996). All analyses were performed using a mixed model procedure (PROC MIXED) of SAS with $\alpha=0.05$.

Indices related to N use (NUE, A_N , MRT, R_E) can be plotted based on the defining variables and the slope of the linear regression denotes the index value. Therefore, we used linear regression (PROC REG) to determine line equations for each species independently and as a function of resource treatment. We used analysis of covariance (PROC MIXED) to compare N use indices (i.e., slopes) of treatments within each species and of species across treatments. We also tested N use indices with ANOVA models identical to those described for [N] and N_C . We analyzed FUE using a similar ANOVA model, but the fixed factor of fertilization was not included.

Results

Nitrogen concentration and nitrogen content

Tissue [N] and N_C were influenced by tissue type, species, fertilization, irrigation, age, and by their interactions. In general, [N] remained within a species-specific operating zone (Fig. 1) and patterns of N_C (Fig. 2) were related to biomass accumulation and not [N]. Here, we focus primarily on predominant treatment and species effects for composite tissue [N] and N_C (Supplemental Table 3). Ephemeral tissues (i.e., fine roots and leaves) exhibited higher [N] than

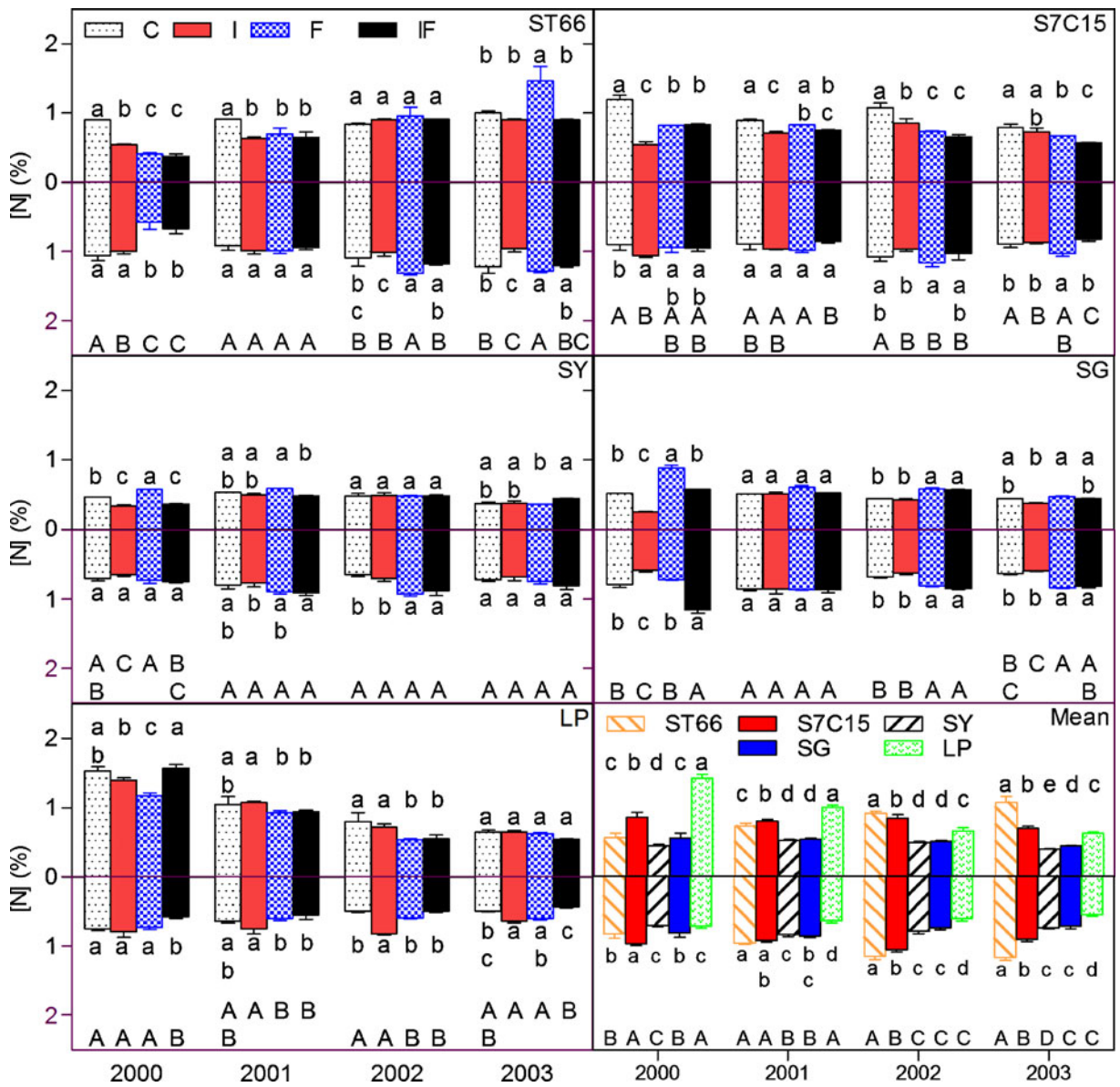


Fig. 1 Aboveground, belowground, and whole-plant [N] (% of dry weight) for ST66, S7C15, sycamore (SY), sweetgum (SG), and loblolly pine (LP) as a function of resource availability and age. Zero on the y axis represents groundline.

Error bars are standard errors for above- and belowground values. Within each year, means with the same letter are not significantly different (Fisher's LSD, $\alpha=0.05$): capital letters refer to whole-plant [N], lowercase letters refer to above- and belowground [N].

perennial tissues and the rank order of perennial tissue [N] depended on species and treatment. Statistical results for composite tissue [N] and N_C are shown in Supplemental Table 3; results for component statistics are in Supplemental Table 4 and 5, and component means by individual year are in Supplemental Tables 6–9 ([N]) and 10–13 (N_C).

Differences in tissue [N] and N_C among species were apparent (Figs. 1 and 2). Species with narrow site requirements (i.e., cottonwoods and sycamore) generally exhibited higher tissue [N] than those with broad site requirements (i.e., sweetgum and loblolly pine), but patterns of tissue N_C did not follow functional groupings. The relative [N] ranking of species within each

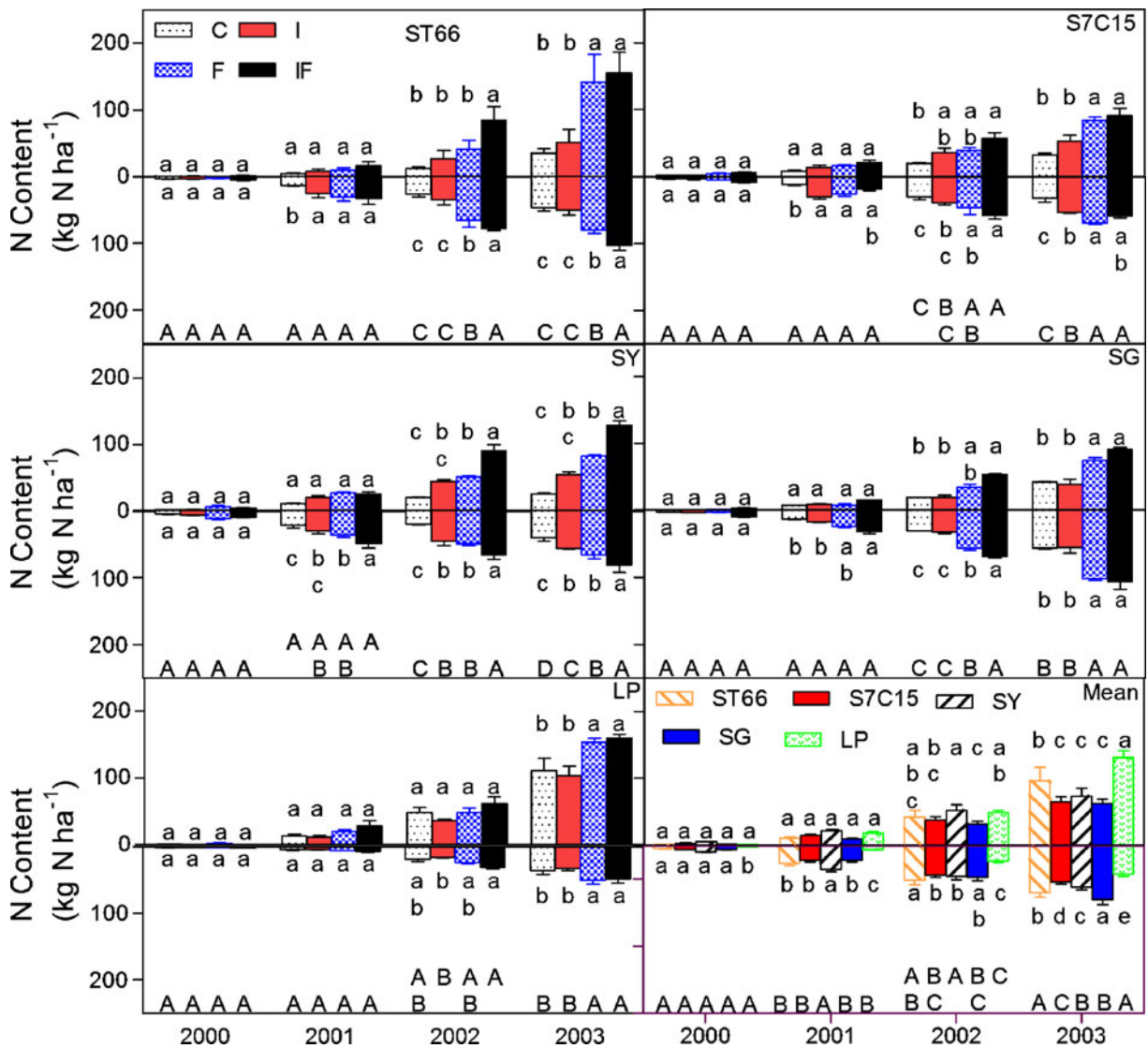


Fig. 2 Aboveground, belowground, and whole-plant N_C (kg N ha^{-1}) for ST66, S7C15, sycamore (SY), sweetgum (SG), and loblolly pine (LP) as a function of resource availability and age; and averaged across treatments (Mean) as a function of age. Zero on the y axis represents groundline. Error bars are standard

errors for above- and belowground values. Within each year, means with the same letter are not significantly different (Fisher's LSD, $\alpha=0.05$): capital letters refer to whole-plant N_C ; lowercase letters refer to aboveground and belowground N_C

functional group was generally consistent, but varied for some component tissues. Similarities in composite tissue N_C existed among species from different functional groups (Fig. 2). Loblolly pine exhibited the largest shoot and total N_C due to perennial foliage.

Resource amendments influenced tissue [N] differently depending on the species and tissue type (Fig. 1; Supplemental Tables 6–9), but influenced N_C consistently within functional groups (Fig. 2). The only component tissue [N] that fertilization consistently

increased in all species (except loblolly pine) was that of leaf. Increases due to fertilization remained within a narrow range of [N] (i.e., 16–46% of C). Irrigation either had no effect or decreased tissue [N]. Fertilization increased N_C of all tissues in all species. Irrigation tended to increase N_C in species with narrow site requirements and either decreased or had no effect on N_C of species with broad site requirements.

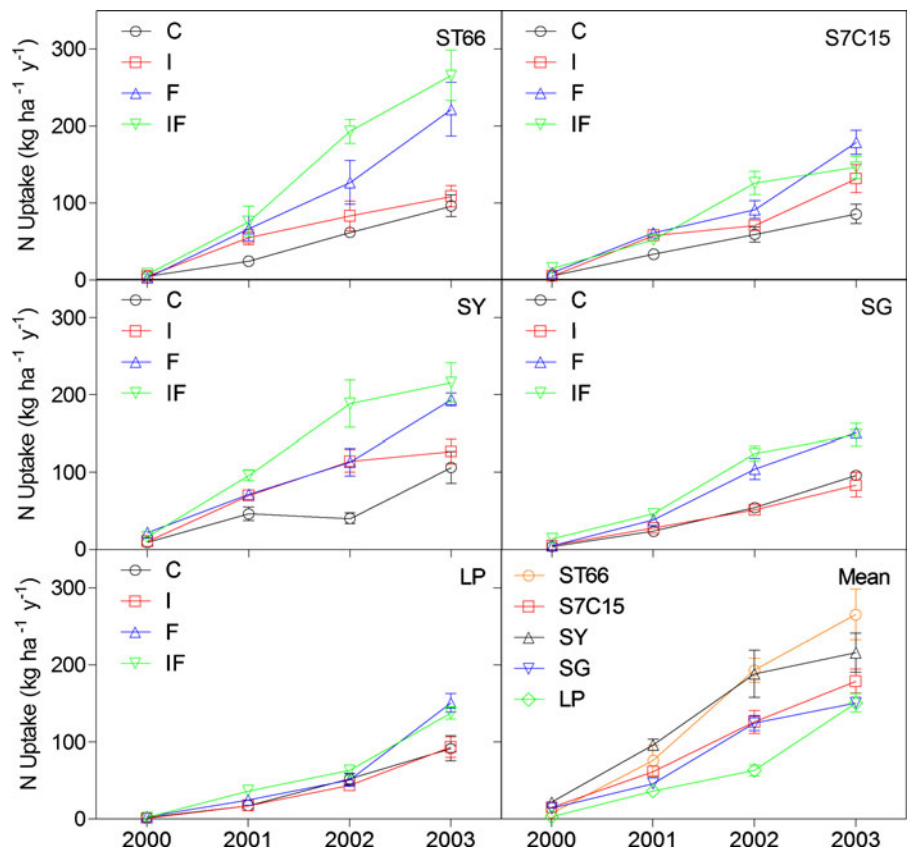
Tissue [N] changed temporally with age, but not in a consistent manner (Fig. 1), whereas N_C increased

with age (Fig. 2). Interactions among treatment factors suggest [N] responses to resource amendments changed with age and varied by species in complex ways, whereas the magnitude of N_C response to resource amendments increased with age and varied among species (i.e., age × species × fertilization × irrigation interaction; Supplemental Tables 3, 10–13). All species appeared to maintain tissue [N] within the bounds of an operating zone (Fig. 1; Supplemental Tables 6–9). Accumulation of N_C followed patterns consistent with biomass accumulation through time and in response to resource amendments.

Nitrogen uptake depends on species group and ephemeral losses

Annual N_{UP} was influenced by species, fertilization, irrigation, age, and by their combinations (Supplemental Table 14). Patterns of annual N_{UP} followed functional groupings, although species and resource amendment effects were not apparent the first growing season (Fig. 3). Narrow site adapted species exhibited higher N_{UP} than broad site adapted species.

Fig. 3 Annual N_{UP} with change over time for ST66, S7C15, sycamore (SY), sweetgum (SG), and loblolly pine (LP) as a function of resource availability; and averaged across treatments (Mean) for each species.

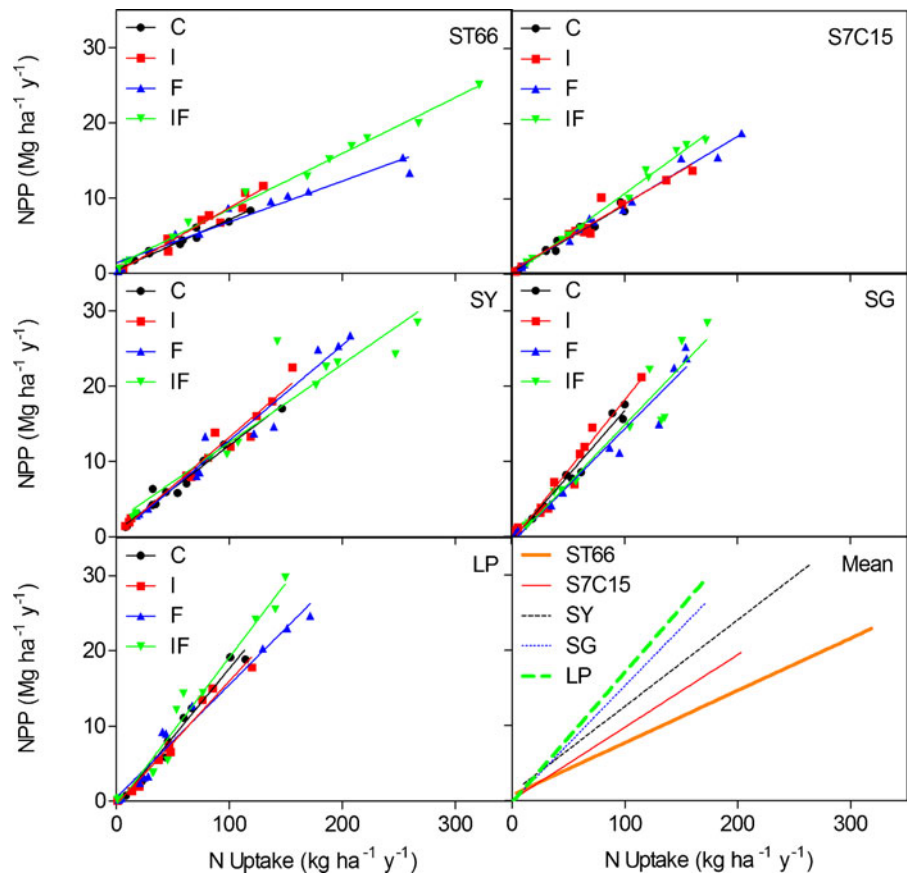


The highest N_{UP} was observed in ST66 and sycamore, whereas loblolly pine and sweetgum exhibited the lowest N_{UP} . The response to resource amendments depended on age and species. The N_{UP} of narrow site adapted species increased with F, I, and IF, although I alone did not continue to increase N_{UP} through the fourth growing season in ST66 and sycamore. Annual N_{UP} of broad-site adapted species increased with F and IF, but not with I alone. Regardless of resource amendments, N_{UP} increased with age in all species.

Indices of efficiency are distinct among functional groups

Species with broad site requirements exhibited higher NUE and A_N than those with narrow site requirements (Figs. 4 and 5). However, patterns of MRT were not consistent with functional groupings as pine exhibited the longest, and ST66 the shortest MRT (Fig. 6). The response of NUE, A_N , and MRT to resource amendments was inconsistent and depended on species (Figs. 4, 5 and 6; Supplemental Tables 14 and 15). In contrast to our hypothesis, NUE did not decrease

Fig. 4 Relationship between NPP and N_{UP} (slope=NUE) as a function of resource availability for ST66, S7C15, sycamore (SY), sweetgum (SG), and loblolly pine (LP); and averaged across treatments (Mean) for each species



with fertilization with the exception of pine (Fig. 4). Irrigation increased NUE in ST66 and IF increased it in S7C15 (Fig. 4). Resource amendments generally did not influence A_N . However, both F and IF decreased A_N in sweetgum, whereas IF decreased it in sycamore (Fig. 5). Resource amendments did not influence MRT except in pine where F decreased it (Fig. 6).

R_E was influenced by species and age, but not resource amendments (Supplemental Table 14). Functional differences in R_E became apparent after the first growing season as species with broad site requirements exhibited higher R_E than those with narrow site requirements. At the end of the fourth growing season, the percent of foliar N retranslocated from senescing leaves was $33.6 \pm 2.3\%$ (mean \pm SE) in S7C15, $38.2 \pm 1.7\%$ in ST66, $43.5 \pm 1.2\%$ in sycamore, $51.6 \pm 2.1\%$ in sweetgum, and $65.6 \pm 1.1\%$ in loblolly pine. Temporal patterns of R_E were not entirely clear. All species experienced highest R_E the first growing season, suppressed R_E the second and third growing seasons, and increased R_E the fourth growing season (data not presented).

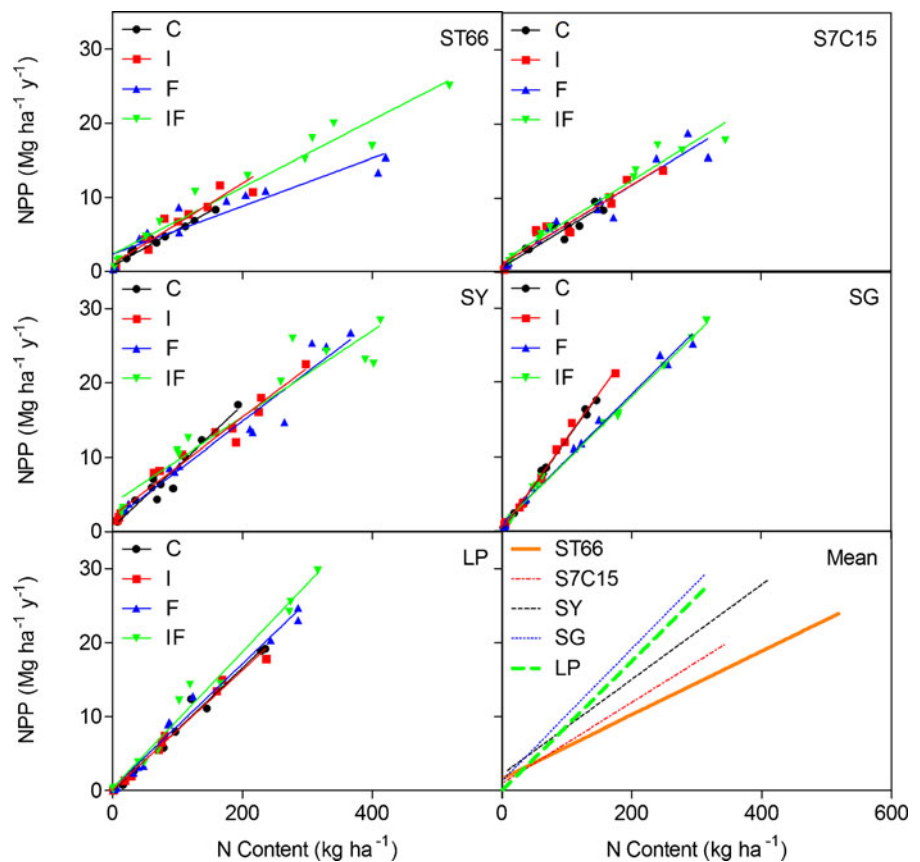
FUE increased with stand development and differed among species; however, relative rankings among species changed through time (i.e., year \times species interaction, $P < 0.0001$). By the fourth growing season, FUE exceeded 75% in all species. There were not clear differences among species by the end of the reporting period as FUE was similar among all species with the exception of ST66 (Fig. 7). Irrigation increased FUE in 2002, but not at any other time (year \times irrigation interaction, Supplemental Table 14). Annual N_{UP} never matched the amount of N_{AV} , with the exception of ST66 in 2003 (Fig. 7). That N_{UP} exceeded N_{AV} indicates that N_{UP} in one or more of the C and I plots underestimated N_{MIN} in F and IF plots, respectively.

Discussion

Nitrogen concentration and nitrogen content

We observed no consistent patterns in the response of [N] to temporal or treatment factors. Others have also

Fig. 5 Relationship between NPP and N_C (slope= A_N) as a function of resource availability for ST66, S7C15, sycamore (SY), sweetgum (SG), and loblolly pine (LP); and averaged across treatments (Mean) for each species



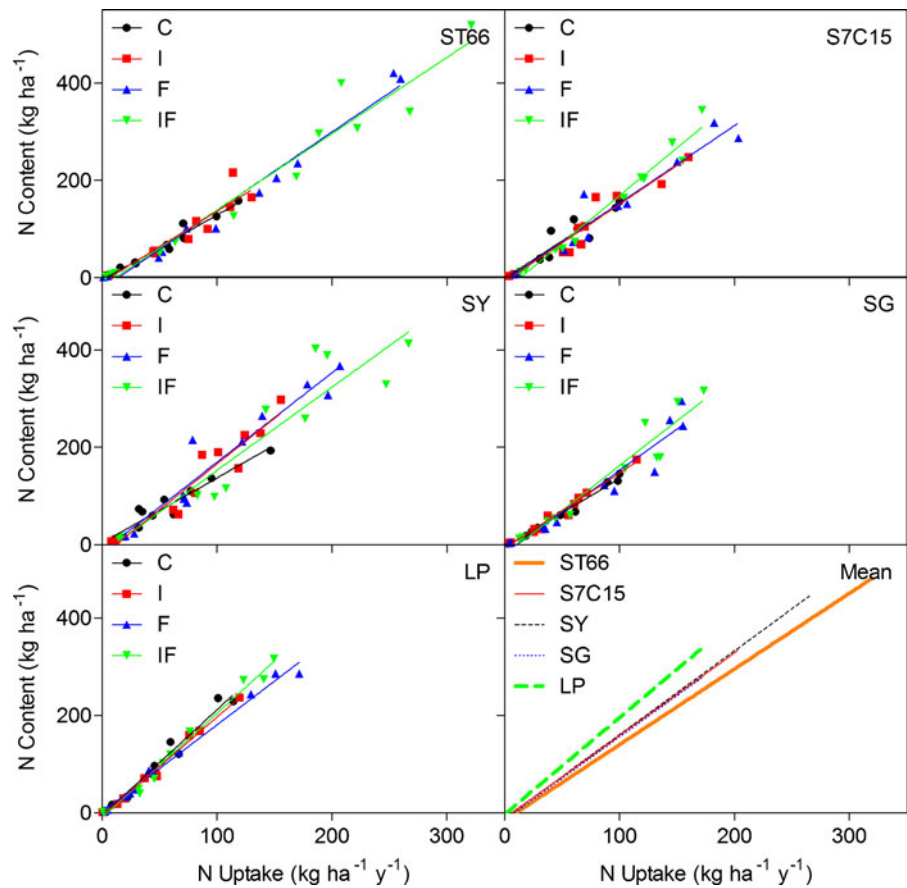
observed relatively constant tissue nutrient concentrations in conjunction with dramatic biomass responses to management treatments in stand-level studies (Borders et al. 2004; Laclau et al. 2000). In our study, each species maintained an equilibrium $[N]$ so that growth resulting from higher N availability diluted $[N]$ to within a species-specific operating range. With limited N availability, growth in our study was relatively low so that $[N]$ remained within the operating range (Ingestad and Kahr 1985). Such narrow $[N]$ ranges indicate plants maintain optimal operating levels to satisfy physiological requirements regardless of nutrient availability. Thus, our results support the hypothesis that equilibrium exists between internal N and carbon—a concept previously observed in controlled environments with herbaceous plants and developed into theoretical models (Lambers 1983; Reynolds and Thornley 1982; Thornley 1972).

N accumulation is correlated with biomass accumulation, and is positively influenced by resource availability (Albaugh et al. 2008; Laclau et al. 2000; Will et al. 2006). Although fertilization elicited a

positive response in N_C and biomass in all species, irrigation either elicited a slight negative response or no response at all for species with broad site requirements. Thus, rates of N accumulation were consistent with species-specific growth rates and were positively influenced by nutrient amendments.

Although foliar $[N]$ is commonly used to indicate nutrient status of forest stands, it is not particularly useful because it is variable, poorly correlated with productivity, and does not reliably predict growth responses to N amendments (Fisher and Binkley 2000; Timmer and Stone 1978). We found canopy N_C was much better correlated with NPP than was leaf $[N]$ and that biomass accumulates to the extent of N availability while maintaining relatively constant $[N]$. Biomass and NPP are highly correlated with leaf area index (leaf surface per unit ground area) and radiation interception (Medlyn et al. 2003). Thus, monitoring leaf area index or radiation interception may better indicate site N status than foliar N (Allen et al. 2005; Coleman et al. 2006; Runyon et al. 1994; Vose and Allen 1988).

Fig. 6 Relationship between N_C and N_{UP} (slope=MRT) as a function of resource availability for ST66, S7C15, sycamore (SY), sweetgum (SG), and loblolly pine (LP); and averaged across treatments (Mean) for each species



Nitrogen uptake

We observed important parallels between above- and belowground resource acquisition. N_{UP} by roots is analogous to photosynthesis by leaves and NUE is the belowground analog of radiation use efficiency. The linear relationship between NPP and intercepted solar radiation is well documented in a variety of forest systems and explains 64–97% of the variation in NPP

(Allen et al. 2005; Cannell et al. 1987; Dalla-Tea and Jokela 1991). Process models rely on this strong correlation between intercepted solar radiation and NPP to estimate stand growth (Medlyn et al. 2003). Strong correlations between NPP and N_{UP} have been reported (Albaugh et al. 2008; Finzi et al. 2007; Norby and Iversen 2006), but generally lack turnover of N in fine roots. We found that N_{UP} derived from a complete budgeting approach was effective in predicting 89–99% of the variation in NPP. These relationships demonstrate the interdependence of N_{UP} , radiation interception, and NPP. Accurate descriptions of forest growth processes regulating NPP should include both N_{UP} and photon absorption. Explaining forest growth through aboveground processes alone discounts the importance of belowground processes and emphasizes the need to incorporate accurate and precise definitions of site N_{AV} .

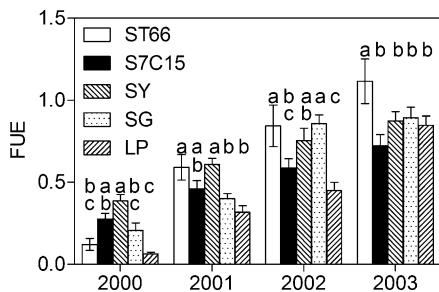


Fig. 7 Fertilizer use efficiency (FUE; Mean±SE) through stand development. Means with the same letter within each year are not significantly different (Fisher's LSD, $\alpha=0.05$)

Increased N_{UP} was largely explained by root biomass and resource amendments. Stable specific N_{UP} (i.e., N_{UP} divided by fine root biomass; data not

presented) indicated N_{UP} and root biomass increased concurrently. Lower N_{UP} in I relative to F and IF shows site nutrient supply capacity (i.e., N_{MIN}) was not enhanced by irrigation and suggests native N supply capacity, not moisture availability (Groffman et al. 2009; Hungate et al. 2007), limited N_{UP} at this site.

Most N_{UP} acquired annually by narrow site adapted species was lost via senescence of ephemeral tissues, while more was retained by broad site adapted species (Fig. 8a). Proportions of N_C lost via ephemeral tissues followed patterns similar to ephemeral losses of N_{UP} (Fig. 8b). Ephemeral N losses were high in hardwoods, ranging from 49% to 78% of N_{UP} in 2003. Ephemeral N losses were dominated by leaf litter in narrow site adapted hardwoods (60–70%) and by fine root turnover in pine (84%). Leaf litter and fine root turnover accounted for similar proportions of ephemeral N loss in sweetgum (48% and 52%, respectively). Ephemeral N losses from sweetgum agree with the 50% ephemeral loss relative to requirement (equivalent to our N_{UP} value) observed by Johnson et al. (2004). Although not the dominant loss in hardwood species, fine root turnover accounted

for 30–52% of ephemeral N losses. Therefore, if fine root turnover is not accounted for when constructing forest N budgets, calculated N_{UP} may underestimate actual N_{UP} by 30–84%. The impact of root turnover on N losses was greater in the trees with high NUE. Our turnover rates for hardwoods (87% of maximum biomass for roots ≤ 1 mm) and pine (110%) were lower than the average of forest fine roots (120%; Gill and Jackson 2000), which suggests the amount of N loss attributed to fine root turnover was smaller than what might be expected from average turnover. The assumption of minimal root R_E (Gordon and Jackson 2000; Nambiar 1987) inflates the amount of N_{UP} lost to root turnover. If retranslocation is occurring (Kunkle et al. 2009), then we expect the proportion of N_{UP} loss to be smaller.

Indices and strategies of efficiency

The species-specific relationships between N_{UP} and NPP were distinct among functional groups, which supports the hypothesis that species with broad site requirements have higher NUE than those with narrow site requirements (Aerts and Chapin 2000; Vitousek 1982). A similar pattern of NUE was reported in a cross-site synthesis of loblolly pine, sweetgum, and various *Populus* spp. grown under ambient and elevated CO_2 (Finzi et al. 2007). In general, NUE appears higher in evergreen than deciduous species (Chapin and Shaver 1989; Gray 1983; Son and Gower 1991).

Narrow site adapted species generally exhibit higher A_N and shorter MRT, compared to broad site adapted species (Aerts and Chapin 2000). In our study, species with broad site adaptations exhibited higher A_N than narrow site adapted species, but patterns of MRT were not consistent within functional groupings. However, MRT was more closely aligned with leaf habit than site adaptation. For example, MRT of deciduous trees ranged from *c.* 1.6 to 1.7 years, whereas MRT of pine was 2.0 years. Our results concur with other reports and suggest an inverse relationship between A_N and MRT does not necessarily apply to species within a narrow range of leaf longevity (Aerts and Decaluwe 1994; Eckstein and Karlsson 2001; Nakamura et al. 2002).

Although not a direct component of the NUE calculation, R_E may indirectly influence NUE by influencing MRT (Escudero et al. 1992). The pattern

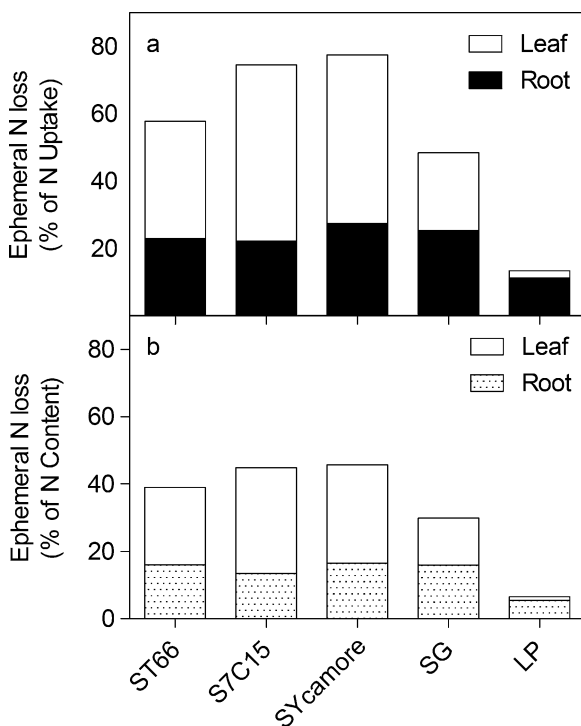


Fig. 8 Mean \pm SE N lost through ephemeral tissues (leaf litter and fine root mortality) in 2003 as a proportion of **a**) annual N_{UP} and **b**) N_C

of R_E among species was similar to those observed with NUE and A_N . Species with broad site requirements were more effective at retranslocating N than were narrow site adapted species. Thus, sweetgum maximized NUE through high A_N and higher R_E , whereas pine maximized NUE through high A_N , higher R_E , and longer MRT. Apparently, the lower R_E of narrow site adapted species is partly responsible for the lower NUE. In other words, perhaps narrow site adapted species are extremely N demanding and confined to sites with high N availability because of poor retranslocation (Killingbeck 1996)

Increased N availability has resulted in decreased NUE for a variety of plant life forms (Birk and Vitousek 1986; de Aldana and Berendse 1997; Lajtha and Klein 1988; Nakamura et al. 2002). However, NUE and its components (A_N and MRT) were not consistently influenced by N availability in our study and R_E was never influenced by N availability. For example, sweetgum maintained the same NUE, regardless of resource amendments whereas NUE of loblolly pine decreased as N availability increased (Fig. 4; Supplemental Table 15). Using a leaf-level NUE index, Birk and Vitousek (1986) also found a reduction in loblolly pine NUE as N availability increased. Aerts and Chapin (2000) showed NUE derived from only aboveground data are not necessarily similar to that derived from whole-plant data. Investigations of NUE in relation to resource availability at the whole-tree level are uncommon and we are only aware of work on saplings (Silla and Escudero 2004, 2006). Few studies have investigated NUE at the whole-tree level (Calfapietra et al. 2007; Finzi et al. 2007; Norby and Iversen 2006), and not as a function of resource availability (Albaugh et al. 2008). Although these studies included some measure of fine root pools, they generally lack estimates of fine root turnover. Based on whole-tree N pools and fluxes, our data suggest the relationship between NUE and resource availability is species dependent.

Much of the applied fertilizer was acquired by trees once they occupied the site (Fig. 7). Calculating the proportion of fertilizer N acquired, or FUE, requires quantification of N_{AV} based on both the amount of N applied via fertilization and N_{MIN} . Although the actual amount of N_{MIN} was unknown, the use of paired fertilized and non-fertilized plot N_{UP} provided approximations of N_{MIN} rates that are comparable to those found by others in the region (Lee and Jose

2006; Gurlevik et al. 2004). Mineralization following fertilization can be higher (Connell et al. 1995) or lower (Johnson et al. 1980), and can depend on the forest type (Lee and Jose 2006), so the magnitude of mineralized N available in fertilized plots was only approximated and some inconsistencies exist. Both N_{UP} and NPP were positively influenced by irrigation, but the lack of an irrigation effect on FUE suggests that, although more N may have been available with irrigation, the amount that could be acquired was not influenced. The increase in FUE with stand development suggests that, as trees occupied the site, their capacity to acquire available nutrients increased. Such increased site resource capture is coincident with reaching stable root length density by 2002 (Coleman 2007).

The high FUE observed here agrees with other studies that applied small but regular nutrient inputs (Ingestad et al. 1981; van Miegroet et al. 1994; Will et al. 2006). Following site occupation, small but regular fertilizer applications are more fully used by forests than single large doses (Johnson 1992). Our FUE values, which exceeded 80%, accounted for below-ground pools and fine root turnover. Aboveground fertilizer recovery by forest trees is typically below 40% (Nason and Myrold 1992). Thus, our results demonstrate the importance of accounting for below-ground N use and suggest that use efficiency is actually much greater than previously estimated based solely on aboveground data.

Application to forest management

Selecting forestry planting stock should consider species adaptability, NPP, and NUE. After four years of growth, species with narrow site requirements had 25% higher NPP and 31% higher N_{UP} than those with broad site requirements. Consequently, narrow site adapted species exhibit greater production potential but will not reach that potential without adequate nutrient supply. On the other hand, species with broad site requirements achieved respectable biomass production without N amendments. Given the environmental and economic costs of fertilizer applications and the universal N limitations on available forestry sites, there are obvious advantages to selecting and planting genotypes with high NUE.

Fast growing hardwoods from bottomland sites with high production potential are promoted for biomass production (Tuskan 1998), but exhibit rela-

tively narrow site requirements which limit potential acreage for planting. In contrast, species with broad site requirements are preferred by silviculturalists due to robust site requirements even though they do not grow as fast as narrow site adapted species under optimal site conditions (Kline and Coleman 2010). Given the large acreage of marginal sites available, species with robust site requirements may produce larger quantities of biomass across the landscape. Higher NUE not only extends the range of potential sites, but also provides greater growth potential for a given value of N_{AV} . Recent emphasis on woody energy crop production suggests that rapid growth should be favored over site adaptability (i.e., increased NPP at the expense of NUE). However, favoring NPP over NUE will effectively limit sites for such plantations and force competition for prime land between food and energy as occurred recently over corn ethanol (Fargione et al. 2008; Searchinger et al. 2008). Rapidly-growing species can be modified or selected to improve resource use efficiencies (Ragauskas et al. 2006).

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